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THE
AMERICAN NATURALIST

Vol. XLVIII September, 1914 No. 573

STUDIES ON INBREEDING. V

Inbreeding and Relationship Coefficients[1]

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In the discussion of inbreeding coefficients contained in a series of recent papers from this laboratory[2] no mention has been made of an important consideration which arises in connection with such coefficients. The further problem, to which we may now turn, may be stated in the following way.

The pedigree of an individual consists of two halves. One of these halves is made up of the sire and his ancestors; the other of the dam and her ancestors. Following the conception of inbreeding set forth in detail in the earlier papers of this series it is plain that the values of the coefficients of inbreeding for a particular pedigree are composed of the following elements.

1. The occurrence of the same individual animals more than once on the sire's side of the pedigree only.

2. The occurrence of the same individual animals more than once on the dam's side of the pedigree only.

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[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 69.

[2] Pearl, R., "Studies on Inbreeding. I. A Contribution Towards an Analysis of the Problem of Inbreeding," Amer. Nat., Vol. XLVII, pp. 577–614, 1913; "The Measurement of the Intensity of Inbreeding," *Me. Agr. Expt. Sta. Bul.*, 215, pp. 123–138, 1913. Pearl, R., and Miner, J. R., "Studies on Inbreeding. III. Tables for Calculating Coefficients of Inbreeding," Me. Agr. Expt. Sta. Ann. Rept. for 1913, pp. 191–202, 1913.

3. The reappearance of animals which appear first on one side of the pedigree (either the sire's or the dam's) on the other side.

If only 1 and 2 are to be found in the pedigree it means that the sire and the dam are totally unrelated (within the limits covered by the pedigree in the particular case). On the other hand, the occurrence of 3 means that sire and dam are in some degree related, and that a portion of the observed inbreeding arises because of that fact. Now the coefficients of inbreeding, in and of themselves, tell nothing about what proportionate part has been played by these three elements in reaching the final result. It is a matter of great importance to have information on this point, because of its genetic significance. It is the purpose of this paper to describe a general method for obtaining this desired information.

The first step in the method, stated briefly, is to break up the pedigree elimination table formed to get the successive values of $p_{n+1} - q_{n+1}$, in our former notation, into four different parts. One of these parts will include the primary reappearance on the sire's side of the pedigree of such animals as appear first on the same side. This may be called the "male only" table. The second part will include the primary reappearance on the dam's side of such animals as first appear on the same side. This is the "female only" table. The third part will include the primary reappearance on the dam's side of such animals as first appear on the sire's side. The fourth part is the reverse of the third. These last two may be called the "cross tables." The sums of the totals of these partial tables will give the total $p_{n+1} - q_{n+1}$ values for the successive generations.

The formation of the tables on this plan may be illustrated with some examples. These examples will also show the skeleton method of writing pedigree elimination tables, which saves much labor. This was referred to, but not significantly illustrated, in the earlier papers. It consists simply in doubling the total of the column for each generation rather than the separate items.

TABLE I

PARTIAL PEDIGREE ELIMINATION TABLE FOR KING MELIA RIOTER 14TH SHOWING THE PRIMARY REAPPEARANCES ON THE SIRE'S SIDE OF THE PEDIGREE OF ANIMALS WHICH FIRST APPEAR ON THAT SIDE

Generation	2	3	4	5	6	7	8	9	10	11	12
Melia Ann's Son			1	(2)[3]							
Melia Ann 3d				1	(6)[3]						
Lucy's Stoke Pogis					3						
Melia Ann					2						
St. Lambert Boy					1						
Letty Rioter					1						
Allie of St. Lambert					1						
Lord Aylmer					1						
Amelia 2d					1	(32)[3]					
Victor Hugo						1					
Oakland's Nora						1					
Stoke Pogis 3d						1					
Bachelor of St. Lambert						1					
Sir George of St. Lambert						1					
Diana's Rioter						1					
Orloff						1					
Lorne						1					
Hugo's Victoria						1	(82)[3]				
Victor Hugo							1				
Pauline							1				
Canada's John Bull							1				
Oakland's Nora							1				
Stoke Pogis 3d							7				
Kathleen of St. Lambert							1				
Lord Lisgar							4				
Lucy of St. Lambert							2				
Diana of St. Lambert							1				
Pet of St. Lambert							1				
Orloff							1				
Bachelor of St. Lambert							1				
Ida of St. Lambert							1	(210)[3]			
Victor Hugo								2			
Stoke Pogis 3d								2			
Lord Lisgar								3			
Lorne								1			
Amelia								1	(438)[3]		
Lord Lisgar									1		
Pride of Windsor									2		
Laval									1		
Amelia									2		
Victor Hugo									3	(894)[3]	
Laval										1	
Amelia										1	
Lisette										1	
Berthe										1	
Totals			1	3	16	41	105	219	447	898	1,796

[3] In this and the following table the numbers in brackets are in each case twice the sum of the numbers in the preceding column. They represent the accumulated ancestral reduplication up to the generation in question.

The pedigree for 12 ancestral generations of the Jersey bull King Melia Rioter 14th (103901) may be taken as the first illustration.

TABLE II

PARTIAL PEDIGREE ELIMINATION TABLE FOR KING MELIA RIOTER 14TH SHOWING THE PRIMARY REAPPEARANCES ON THE DAM'S SIDE OF THE PEDIGREE OF ANIMALS WHICH FIRST APPEAR ON THAT SIDE

Generation	2	3	4	5	6	7	8	9	10	11	12
King's Rioter Lad	—	—	—	1	2	4	8	16	32	64	128

Table III is clearly the one which demands special attention. As will shortly appear, it is the most important for the theory of inbreeding. Let us attempt its analysis. Just what does the first entry mean genetically? It states that King Melia Rioter, an animal which first appeared on the sire's side of the pedigree, reappeared in the second ancestral generation on the dam's side. What this clearly means is that at least one half of all the dam's ancestors, in the third and higher ancestral generations, *are identically the same animals as are ancestors of the*

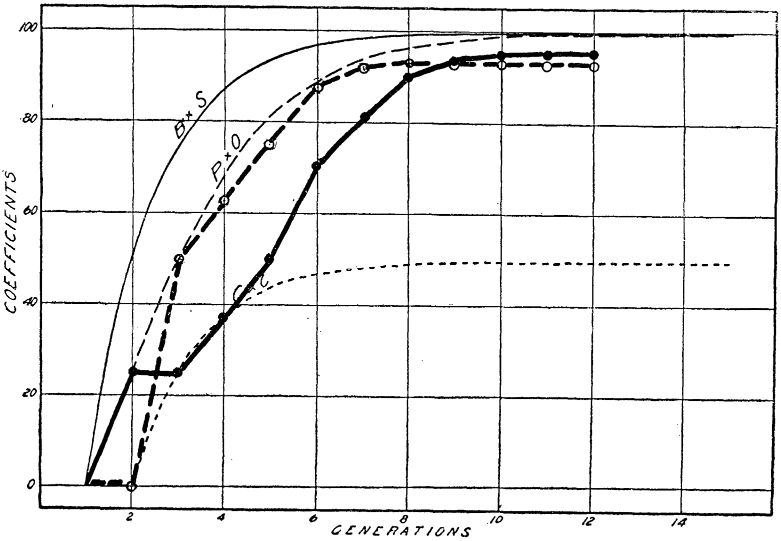

FIG. 1. Diagram showing (*a*) the total inbreeding (heavy solid line) and (*b*) the relationship (heavy broken line) curves for the Jersey bull, King Melia Rioter 14th. The high order of the inbreeding and relationship between the sire and dam in this case is evident by comparison with the lighter lines, which give the maximum values for continued brother × sister, parent × offspring and cousin × cousin breeding.

sire. The next entry in Table III indicates that in the fourth and higher ancestral generations at least 5/8 of all the dam's ancestors were the same individual animals as were also ancestors of the sire. One half of them were the same before the reappearance of St. Lambert's Rioter King. He makes up the additional 1/8 of the dam's ancestry.

TABLE III

Partial Pedigree Elimination Table for King Melia Rioter 14th Showing the Primary Reappearances on the Dam's Side of the Pedigree of Animals which first Appear on the Sire's Side

Generation	2	3	4	5	6	7	8	9	10	11	12
King Melia Rioter	1	(2)	(4)	....	....	....	....	....	....	....	....
St. Lambert's Rioter King	..	...	1	(10)	....	....	....	....	....	....	....
King of St. Lambert	..	...	...	1	....	....	....	....	....	....	....
St. Lambert Boy	..	...	...	1	(24)	....	....	....	....	....	....
St. Lambert Boy	..	...	...	....	2	....	....	....	....	....	....
Oakland's Nora	..	...	...	....	1	....	....	....	....	....	....
St. Lambert's Rioter King	..	...	...	....	1	(56)	....	....	....	....	....
St. Lambert Boy	..	...	...	....	....	1	....	....	....	....	....
King of St. Lambert	..	...	...	....	....	1	....	....	....	....	....
St. Lambert's Letty	..	...	...	....	....	1	(118)	....	....	....	....
Letty Coles 2d	..	...	...	....	....	....	1	(238)	....	....	....
King of St. Lambert	..	...	...	....	....	....	....	1	....	....	....
Louise's Grace	..	...	...	....	....	....	....	1	....	....	....
Totals	1	2	5	12	28	59	119	240	480	960	1,920

From these tables it is obvious that a very considerable portion of the inbreeding shown in the pedigree of King Melia Rioter 14th arises from the fact that his sire and dam were closely related. Furthermore, both sire and dam are closely inbred in their own lines. The curve of total inbreeding in this case is shown in Fig. 1, along with the curves for continued brother × sister, parent by offspring, and cousin × cousin mating.

TABLE IV

Summarized Pedigree Elimination Table for King Melia Rioter 14th

Generation	2	3	4	5	6	7	8	9	10	11	12
♂ only			1	3	16	41	105	219	447	898	1,796
♀ only				1	2	4	8	16	32	64	128
Cross-over	1	2	5	12	28	59	119	240	480	960	1,920
Together	1	2	6	16	46	104	232	475	959	1,922	3,844

From this we have, for the inbreeding coefficients,

$Z_0 = 0$
$Z_1 = 25.00$
$Z_2 = 25.00$
$Z_3 = 37.50$
$Z_4 = 50.00$
$Z_5 = 71.88$
$Z_6 = 81.25$
$Z_7 = 90.63$
$Z_8 = 92.77$
$Z_9 = 93.65$
$Z_{10} = 93.85$
$Z_{11} = 93.85$

These facts will possibly be made clearer to those not actually working much with pedigrees by Table V, which gives the first four ancestral generations[4] of the pedigree of King Melia Rioter 14th.

Generalizing the above reasoning we get the following result.

In A_3, and higher ancestral generations, $2/4 = 50.00$ per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_4, and higher ancestral generations, $5/8 = 62.50$ per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_5, and higher ancestral generations, $12/16 = 75.00$ per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_6, and higher ancestral generations, $28/32 = 87.50$ per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_7, and higher ancestral generations, $59/64 = 92.19$ per cent. of the dam's ancestors are animals which are also ancestors of the sire.

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[4] In the study of pedigrees stress is naturally laid on the ancestral generations, rather than on the filial, as in breeding experiments. It becomes very convenient to have a brief designation for ancestral generations, in the same way that F_1, F_2, etc., are used to denote filial generations. I would suggest the use of the letter A with sub-numbers for this purpose. We then have A_1 denoting the parental generation, A_2 the grandparental, A_3 the great-parental, etc.

In A_8, and higher ancestral generations, 119/128 = 92.97 per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_9, and higher ancestral generations, 240/256 = 93.75 per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_{10}, and higher ancestral generations, 93.75 per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_{11}, and higher ancestral generations, 93.75 per cent. of the dam's ancestors are animals which are also ancestors of the sire.

In A_{12}, and higher ancestral generations, 93.75 per cent. of the dam's ancestors are animals which are also ancestors of the sire.

TABLE V

PEDIGREE FOR FOUR ANCESTRAL GENERATIONS OF KING MELIA RIOTER 14TH

Sex ♂ King Melia Rioter 14th. No. 103901	♂ King Melia Rioter. No. 73104	No. 63200 ♂ Marjorie Melia Ann's Son.	No. 56581 ♂ Melia Ann's King.	No. 22041 ♂ Melia Ann's Son.
				No. 100775 ♀ Lottie Melia Ann.
			No. 157263 ♀ Marjorie Melia Ann.	No. 22041 ♂ ● Melia Ann's Son.
				No. 905883 ♀ Mary Melia Ann.
		No. 181544 ♀ Letty Silver Hair.	No. 58169 ♂ King of All Kings.	No. 54896 ♂ St. Lambert's Rioter King.
				No. 114804 ♀ St. Lambert's Letty.
			No. 148456 ♀ Exile's Silver Hair.	No. 32559 ♂ Exile of St. Anne's.
				No. 60449 ♀ Silver Hair 4th.
	♀ Larissa Marie. No. 262926	No. 73104 ♂ ● King Melia Rioter.	No. 63200 ♂ ⊗ Marjorie Melia Ann's Son.	No. 56581 ♂ ⊗ Melia Ann's King.
				No. 157263 ♀ ⊗ Marjorie Melia Ann.
			No. 181544 ♀ ⊗ Letty Silver Hair.	No. 58169 ♂ ⊗ King of All Kings.
				No. 148456 ♀ ⊗ Exile's Silver Hair.
		No. 219360 ♀ Dula Riotress Maid.	No. 62098 ♂ King Rioter's Lad.	No. 54896 ♂ ● St. Lambert's Rioter King.
				No. 142296 ♀ King's Riotress Nora.
			No. 218796 ♀ St. Lambert's Dula Riotress.	No. 57778 ♂ St. Lambert's Boy.
				No. 174761 ♀ Rioter Lad's First Daughter.

These percentages are quantities of a good deal of interest. They measure the degree in which King Melia Rioter 14th's sire and dam were related to each other. Community of ancestry is the basis of kinship.

Percentages derived in the way shown above, from cross pedigree elimination tables, I propose to call *coefficients* of relationship, and to designate by the letter K, with appropriate sub-numbers referring to the generation. These relationship coefficients are, with some limitations, independent of the inbreeding coefficients in the values they may take, though the two will usually be correlated to some degree. It is, however, possible to have a high value of Z with $K = 0$.

TABLE VI

COMPARING THE MAXIMUM POSSIBLE VALUES OF THE COEFFICIENTS OF INBREEDING (Z) WHEN THE COEFFICIENT OF RELATIONSHIP K EQUALS (a) ZERO, AND (b) 100

Generation	Maximum Possible Value of Z when $K = 0$	Maximum Possible Value of Z when $K = 100$
A_1	0	0
A_2	0	50.00
A_3	50.00	75.00
A_4	75.00	87.50
A_5	87.50	93.75
A_6	93.75	96.88
A_7	96.88	98.44
A_8	98.44	99.22
A_9	99.22	99.61
A_{10}	99.61	99.80

The most important feature of the relationship coefficients is found in their genetic implications. This can be indicated best by an illustration. Let us consider the case of the maximum possible degree of inbreeding with $K = 0$. This will be found when the sire and the dam are each inbred to the highest possible degree (continued brother × sister mating) but are in no way related to each other. Such a case would be afforded, for example, if a Jersey bull, the product of continued brother × sister mating, was bred to a Holstein cow, which was also the product of a continued brother by sister breeding. Clearly K would be 0, since no animal on one half of the pedigree could even appear on the other. The values of the successive coefficients of inbreeding (Z's) in such a case are shown in Table VI, where they are compared with the coefficients of inbreeding in complete continued brother × sister mating, where $K = 100$.[5]

From this it appears that an individual may be inbred in 10 generations to within two tenths of one per cent. as intensely, measured by the coefficients of inbreeding, if his sire and dam are in no way related, as he would be if his sire and dam were brother and sister. But clearly the germinal constitution of the individual produced would, except by the most remote chance, be quite different in the two cases. This point is so evident as to need no elaboration. It has been brought out by East and Hayes.[6]

The values of the K's for a particular pedigree evidently furnish a rough index of the probability that the two germ-plasms which unite to form an individual are alike in their constitution. This will follow because of the fact that the probability of likeness of germinal constitution in two individuals must tend to increase as the number of ancestors common to the two increases. Just what is the law of this increase in probability is a problem in Mendelian mathematics which has not yet been worked out. The general fact, however, seems quite sure.

From the above discussion it seems plain that in reaching a numerical measure of the degree of inbreeding it is not sufficient to consider coefficients of inbreeding alone. The coefficients of relationship must also be taken into account.

It is suggested that the two constants be written together for each generation, the coefficient of inbreeding being followed by the coefficient of relationship in brackets. Thus we have

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[5] Since, of course, *all* of a sister's ancestors are identical with her brother's.

[6] U. S. Dept. Agr. Bur. Plant Industry, Bul. No. 243, pp. 1–58, 1912.

INBREEDING AND RELATIONSHIP COEFFICIENTS OF KING MELIA RIOTER 14TH

$Z_0 (K_1) = 0 \quad (0)$
$Z_1 (K_2) = 25 \quad (0)$
$Z_2 (K_3) = 25.00 \quad (50.00)$
$Z_3 (K_4) = 37.50 \quad (62.50)$
$Z_4 (K_5) = 50.00 \quad (75.00)$
$Z_5 (K_6) = 71.88 \quad (87.50)$
$Z_6 (K_7) = 81.25 \quad (92.19)$
$Z_7 (K_8) = 90.63 \quad (92.97)$
$Z_8 (K_9) = 92.77 \quad (93.75)$
$Z_9 (K_{10}) = 93.65 \quad (93.75)$
$Z_{10} (K_{11}) = 93.85 \quad (93.75)$
$Z_{11} (K_{12}) = 93.85 \quad (93.75)$

The physical meaning of these expressions is simple and straightforward. $Z_4(K_5)$ tells us that in the 5th ancestral generation of King Melia Rioter 14th he had only one half as many different ancestors as was possible for that generation, and of his ancestors three fourths were common to his sire and his dam. However one looks at the matter there can be no denial that King Melia Rioter 14th is a closely inbred animal.

In Fig. 1 the heavy broken line gives the relationship coefficients for King Melia Rioter 14th. It will be instructive now to consider another example by way of contrast. Again a Jersey bull, Blossom's Glorene (102701), will be taken. Only the final result need be given.

INBREEDING AND RELATIONSHIP COEFFICIENTS OF BLOSSOM'S GLORENE

$Z_0(K_1) = 0 \quad (0)$
$Z_1(K_2) = 0 \quad (0)$
$Z_2(K_3) = 12.50 \quad (0)$
$Z_3(K_4) = 12.50 \quad (0)$
$Z_4(K_5) = 25.00 \quad (0)$
$Z_5(K_6) = 29.69 \quad (0)$
$Z_6(K_7) = 35.94 \quad (0)$
$Z_7(K_8) = 40.23 \quad (0)$

The total inbreeding and the relationship curves are given in Fig. 2.

The difference in the breeding of this bull and the one considered in the former example is striking. In the 8th ancestral generation Blossom's Glorene has but 60 per cent. of the number of different ancestors possible in that generation, but not one single animal in the ancestry of his sire occurs in the ancestry of his dam (within the limits A_1 to A_8). The probability is that Blossom's Glorene is heterozygous in respect of most of his characters, while King Melia Rioter 14th is homozygous.

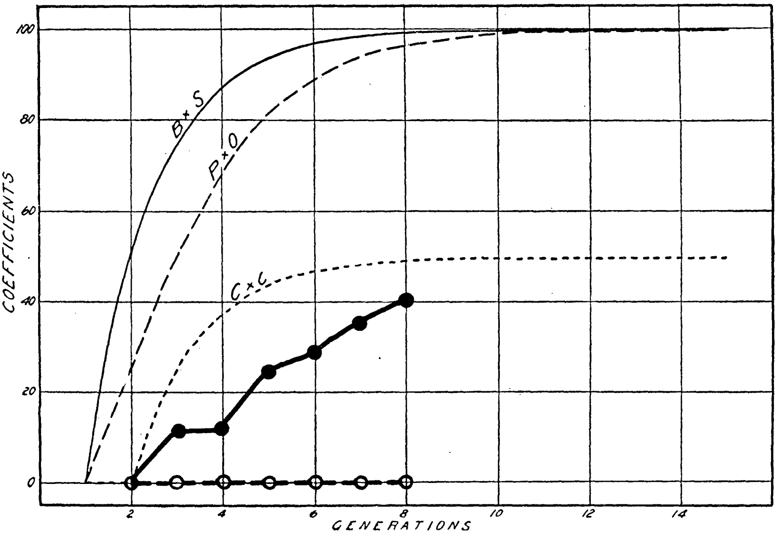

FIG. 2. Diagram showing the total inbreeding (heavy solid line) and the relationship (heavy broken line) curves for the Jersey bull Blossom's Glorene, over a period of eight ancestral generations. Compare with Fig. 1.

SUMMARY

The object of this paper is to call attention to the fact that inbreeding of considerable degree may exist in the entire absence of any kinship between the two individuals bred together, and to bring forward a method of separately measuring what proportion of the observed inbreeding in a particular case is due to kinship of the parents, and what to earlier ancestral reduplication. A proposed coefficient of relationship is described, and its application illustrated by concrete cases.